Oecologia (Berlin) (1983) 60:10–17

Oecologia

Ecophysiology of *Yucca brevifolia*, an arborescent monocot of the Mojave Desert

Stanley D. Smith,* Terry L. Hartsock, and Park S. Nobel

Department of Biology and the Laboratory of Biomedical and Environmental Sciences, University of California, Los Angeles, CA 90024, USA

Summary. Photosynthetic characteristics and transpiration of *Yucca brevifolia*, an evergreen tree endemic to the Mojave Desert of California and Nevada, were examined in the field and the laboratory. *Yucca brevifolia* was confirmed to be a C_3 plant, with no CAM tendencies observed for its semi-succulent leaves. The species exhibited a maximum net CO_2 uptake of 12 μmol m^{-2} s^{-1} at 22° C when grown at day/night air temperatures of 31° C/17° C (data expressed on a total area basis for these opaque leaves). The optimum temperature for CO_2 uptake shifted 4.5° C per 10° C change in daytime growth temperature, so that observed leaf temperatures in the field were near optimum temperatures throughout the midday period in all but the hottest months of the year. Leaves also acclimated to low and high temperature extremes, tolerances ranging to −11° C and to 59° C, respectively, suggesting that low temperatures limit the distribution of *Y. brevifolia* but high temperatures do not. Light saturation of photosynthesis occurred at a relatively low PAR of about 500 μmol m^{-2} s^{-1}, similar to the actual PAR within a rosette. Diurnal patterns of leaf conductance shifted from a broad midday peak in wet seasons to a reduced, narrow, early morning peak in the dry season, indicating effective stomatal control of water use. The approximately 5-month-long winter-spring growth season accounted for 80% of the yearly CO_2 uptake, with a predicted annual uptake of about 22 mol m^{-2} y^{-1} and a transpiration ratio of 700.

Introduction

Yucca brevifolia Engelm. var. *brevifolia*, commonly known as the Joshua tree, is a monocotyledonous evergreen tree considered to be the most characteristic plant of the Mojave Desert of North America (Benson and Darrow 1981). It forms dense "forests" over much of its range, and is the largest non-riparian plant of the Mojave Desert, reaching a height of up to 15 m (Munz 1974). Numerous narrow, but thick, linear leaves are borne in large rosettes which occur at the apex of the trunk or its branches. The leaves are evergreen, though little is known about their longevity. The large leaf surface area maintained throughout the year in some of the driest habitats in North America suggests that *Y. brevifolia* is well adapted to seasonal water stress. The species produces large quantities of fruit in wet years and could become a commercially important source of both seed oil and sapogenins from native stands or orchards (Gentry 1980).

Yucca brevifolia has been placed within the Agavaceae (Munz 1974) and the Liliaceae (Benson and Darrow 1981). It is closely related to a number of evergreen rosette species in the deserts of North America belonging to the genera *Agave*, *Dasylirion*, and *Nolina*. All of these species possess an evergreen rosette that lives for several to many years prior to the formation of a terminal inflorescence. In *Y. brevifolia*, branching occurs at the sites where the inflorescences are produced, eventually leading to a multi-rosette plant with a distinct tree-like form.

Until recently, little has been known about the physiology of *Yucca* species or their photosynthetic pathways. It has been assumed that *Yucca* species were Crassulacean acid metabolism (CAM) plants (Bender et al. 1973; Syvertsen et al. 1976), with Johnson (1975) listing *Y. brevifolia* as a CAM plant. However, a recent study of evergreen rosette plants from the Chihuahuan Desert (Kemp and Gardetto 1982) has indicated that narrow-leaved yuccas are C_3, while the broad-leaved, more succulent yuccas exhibit CAM similar to agaves (e.g., Szarek and Troughton 1976; Nobel and Hartsock 1978). Our study confirms that *Y. brevifolia* exhibits C_3 photosynthesis, and also attempts to quantify photosynthesis and transpiration of the species as a function of various environmental parameters. In addition an assessment was made of the seasonal and yearly productivity and transpiration of *Y. brevifolia*. Its relatively large size and presumably old age in communities essentially devoid of other large plant species suggests that *Y. brevifolia* is quite tolerant to temperature extremes, and so a secondary objective of this study was to ascertain environmental limits on the distribution of the species by examining its tolerances to high and low temperatures.

Materials and methods

Plants

Field studies were conducted in Lost Horse Valley, Joshua Tree National Monument, California, at 34°02′N latitude, 116°09′W longitude, 1,355 m elevation. The site is a gently sloping alluvial fan with sandy soil. Although *Y. brevifolia*

* *Present address:* Bioresources Center, Desert Research Institute, P.O. Box 60220, Reno, Nevada 89506, USA

Offprint requests to: P.S. Nobel

was the most conspicuous plant on the site, vegetation cover was dominated by a perennial grass (*Hilaria rigida*) and several small shrubs (primarily *Coleogyne ramosissima, Eriogonum fasciculatum*, and *Gutierrezia microcephala*). A non-branched individual plant was selected for the majority of field measurements, although other plants were periodically monitored for comparative purposes. Leaf area of the study plant was based on the total number of green leaves and the area of individual sampled leaves, which was measured with a Lambda Instruments LI-3000 portable leaf area meter. Chlorophyll was extracted separately from each surface of fresh leaf cores and assayed in 80% acetone/20% water (v/v). Dry weight was determined after drying leaves at 80° C for 48 h.

For laboratory studies, four-year-old 0.5-m-tall plants of *Y. brevifolia* germinated from seed collected at the U.S. Department of Energy Nevada Test Site in southern Nevada were utilized in the gas exchange measurements, while young 1.0-m-tall *Y. brevifolia* transplanted from near the field site were utilized in the temperature tolerance experiments. Experimental plants were grown individually in equal mixtures of sand and desert soil in growth chambers programmed for 14-h days and several thermal regimes. Photosynthetically active radiation from 400 to 700 nm (PAR) averaged 450 μmol m^{-2} s^{-1} (23 mol m^{-2} d^{-1}) on the adaxial leaf surfaces and 300 μmol m^{-2} s^{-1} (15 mol m^{-2} d^{-1}) on the abaxial surfaces, and was provided by cool-white fluorescent lights supplemented with tungsten filament lamps. The relative humidity in the chambers was $40 \pm 10\%$ during the daytime and $60 \pm 10\%$ at night, and the wind speed averaged 0.3 m s^{-1}. Plants were watered weekly with 0.1 strength Hoagland's no. 1 solution plus micronutrients so that the soil water potential near the roots was -0.2 ± 0.1 MPa.

Gas exchange

Net photosynthesis and leaf water vapor conductances were measured in the laboratory in a modified Siemens null-point compensating closed-circuit flow system (Nobel and Hartsock 1978). Carbon dioxide concentrations were determined with an Anarad AR-500R infrared gas analyzer and water vapor concentrations with a Cambridge Systems EG & G 880 dewpoint hygrometer. Two entire attached leaves were sealed into an assimilation chamber containing 340 $\mu l\ l^{-1}$ CO_2 and 10 g m^{-3} water vapor in air. PAR normal to the planes of the leaves was adjusted to be approximately equal for adaxial and abaxial surfaces. The water vapor conductance equaled the net rate of water loss per unit total leaf surface area divided by the water vapor concentration drop from leaf to air; total leaf surface area was used for *Y. brevifolia*, due to its thick opaque leaves. The CO_2 residual conductance equaled the net rate of CO_2 uptake per unit total leaf surface area divided by the CO_2 concentration in the intercellular air spaces just interior to the stomata (Nobel and Hartsock 1979). PAR and temperature responses were determined for plants grown for two weeks in three different day/night growth temperatures: 20° C/9° C, 31° C/17° C and 40° C/25° C, representing the maximum/minimum air temperatures at the study site in late winter, late spring, and mid-summer, respectively.

Leaf conductance to water vapor was determined in the field throughout whole days on a bimonthly basis, commencing in November 1981. Measurements were made using a Lambda Instruments LI-60 diffusive resistance porometer with an LI-20S sensor (calibrated prior to each set of measurements) and with a Lambda Instruments LI-1600 steady state porometer. The water vapor content of the air was determined with a Weather Measure H311 hygrothermograph. Leaf temperature was measured with an Everest Interscience 210 infrared thermometer with a 4.5 mm diameter focus. Leaf transpiration was defined as the leaf water vapor conductance times the water vapor concentration difference from leaf to ambient air, assuming that the air inside the leaf was saturated with water vapor at the leaf temperature. Daily transpiration was the mean leaf transpiration for 12 leaf surfaces (6 adaxial and 6 abaxial) determined approximately hourly and integrated diurnally. Leaf osmotic potentials were obtained by placing a small amount of macerated chlorenchyma tissue in a Wescor C-52 leaf chamber used in conjunction with a Wescor HR-33T dewpoint microvoltmeter. Soil water potentials were monitored in the vicinity of the test plant at 10 and 40 cm depths with Wescor PT 51-05 soil thermocouple psychrometers (in triplicate at each depth). Measurements of leaf osmotic potential and soil water potential were made at dawn.

PAR interception by the single-rosette test plant was determined in the field with a Lambda Instruments LI-190S quantum sensor. Four leaves, one in each cardinal direction, were tagged in each of three rosette whorls (upper, middle, and lower). PAR was measured hourly at midleaf in the plane of each tagged leaf for both adaxial and abaxial surfaces, thus giving incident PAR for 24 leaf surfaces per measurement period.

Thermal tolerance

Thermal tolerances of *Y. brevifolia* were examined by subjecting leaves to high and low temperature treatments for plants maintained under stepwise increasing day/night air temperatures. After two weeks at 15° C/5° C, the heat and cold tolerances were tested, and then the growth temperatures were raised by 15° C. High temperature treatments were done by immersing detached leaves at least 6 cm long (wrapped in plastic) in waterbaths with temperatures ranging from 25° C to 65° C ($\pm 0.2°$ C) for one hour, after which the leaves were cooled to 25° C before assaying for heat damage. Low temperature treatments were done by placing detached leaves in a deep freeze (Revco ULT-385A) and lowering the air temperature by 2° C/h. Leaves were removed hourly (i.e., at 2° C intervals), warmed in air to 23° C, and then assayed for cold damage.

Thermal tolerance of the leaf photosynthetic machinery was ascertained by determining the temperature at which the chlorophyll fluorescence yield was substantially increased (Schreiber and Berry 1977). Chlorophyll fluorescence induction kinetics were determined at 23° C with a Brancker Research SF-20 fluorometer. Thermal tolerance of cellular membranes was evaluated by measuring the percentage of chlorenchyma cells that took up a stain (neutral red), which is accumulated in the vacuoles of living cells only (Onwueme 1979). For each test at least 500 cells in the upper 5 cell layers of the chlorenchyma were examined per leaf on 10 fresh sections 1 to 2 cell layers thick (70 μm) at a magnification of 400× using a Zeiss phase-contrast research microscope. Fresh sections were placed in 0.3 mM (0.01% by weight) neutral red (3-amino-7-dimethyl-amino-

2-methylphenazine (HCl)) for 5 min prior to observation. Thermal tolerance for staining was defined as the temperature at which a 50% reduction occurred in the percentage of cells taking up neutral red relative to controls.

Results

Morphology, microclimate, and PAR interception

Morphological parameters for the single-rosette plant of *Y. brevifolia* on which leaf conductance and PAR interception measurements were made are presented in Table 1. The plant had 560 evergreen opaque leaves arranged in a rosette occurring above a 0.5 m leafless trunk. The rosette projected onto approximately 0.09 m^2 of ground area, resulting in a conventional leaf area index (one side) of 9.1. The fresh to dry weight ratio (in September 1982) was 2.07 ± 0.02. On the experimental plant, the uppermost 11% of the leaves were oriented within 30° of vertical, the middle 83% were oriented at 30° to 60°, and the lowermost 6% were within 30° of horizontal. Individual leaves apparently remain green at least 4 years, and increase in specific leaf weight and chlorophyll content as they age (Table 1). Chlorophyll content was slightly, but not significantly, higher for the abaxial surfaces.

The maximum/minimum air temperatures, monthly precipitation, soil water potentials, and leaf osmotic potentials during the measurement period are presented in Fig. 1. The Mojave Desert typically has moist winters and a dry spring, with late summer precipitation usually occurring. The 1981–1982 season was typical of the above pattern, as the yearly precipitation of 100 mm was distributed approximately equally for the January to May (45 mm) and July to September (55 mm) periods. January and March rainfall resulted in moist soils well into the spring at both 10 and 40 cm depths (Fig. 1). Soils began drying appreciably in May, and soil water potential dropped rapidly thereafter, becoming less than −6.0 MPa at both depths by mid-July. Summer rainfall commencing in late July wetted the soil at 10 cm, but not at 40 cm, for the September measurement period. Leaf osmotic potentials reflected seasonal variation in soil water potentials (Fig. 1) and were similar to water potentials for other non-succulent yuccas (Kemp and Gardetto 1982). Leaf osmotic potential appeared to remain above soil water potential for a substantial period of the year, from early- or mid-summer to the start of the winter rains.

Ambient PAR and canopy PAR interception are given for three representative times of the year in Fig. 2. Leaf PAR interception averaged for each side of the opaque leaves exceeded 50% of the PAR incident on a horizontal surface at the beginning and end of the day. At midday, leaf PAR interception averaged 35% of horizontal PAR in November and about 28% in March and July. The tendency for leaves to become progressively more horizontal with age (and located farther down in the rosette), together with a non-overlapping leaf arrangement in successive whorls, results in effective light penetration into the rosette, even during times of high solar elevation. In March, total daily PAR incident on a horizontal surface was 43.2 mol m^{-2} d^{-1} on a clear day. The total daily PAR averaged for both sides of the leaves was 15.1 mol m^{-2} d^{-1} in the upper canopy, 9.3 mol m^{-2} d^{-1} in the middle canopy, and 8.5 mol m^{-2} d^{-1} in the lower canopy. The percentage of total leaf PAR intercepted by the adaxial surface was 62% in the upper canopy, 48% in the middle canopy, and 52% in the lower canopy.

Table 1. Morphological characteristics of the young *Y. brevifolia* with a single rosette, which was used in the field analyses. Measurements were made on 15 September 1982. Leaf properties are based on a sample size of 30 (4 for chlorophyll measurements) and are expressed as mean ± 1 SD

Plant and rosette properties	
Plant height	1.32 m
Rosette	
length	0.82 m
diameter	0.34 m
dry weight	0.95 kg
Number of leaves	560
Total leaf area (both sides)	1.66 m^2
Leaf properties	
Length	164 ± 13 mm
Width (midlength)	8.1 ± 0.6 mm
Thickness (midlength)	3.94 ± 0.11 mm
Surface area (one side)	0.00148 ± 0.00017 m^2
Specific weight (dry)	
upper part of rosette	1.03 ± 0.03 kg m^{-2}
middle of rosette	1.17 ± 0.03 kg m^{-2}
lower part of rosette	1.30 ± 0.05 kg m^{-2}
Chlorophyll	
young leaf, adaxial surface	386 ± 71 mg m^{-2}
young leaf, abaxial surface	420 ± 80 mg m^{-2}
old leaf, adaxial surface	510 ± 36 mg m^{-2}
old leaf, abaxial surface	556 ± 68 mg m^{-2}

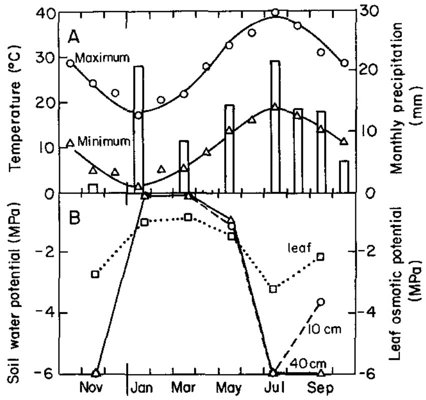

Fig. 1 A, B. Climatic and water potential measurements in the field for various times during the year: **A** daily mean maximum and minimum air temperatures, and monthly precipitation; and **B** soil water potential at 10 cm and 40 cm depths, and leaf osmotic potential for each measurement date

Leaf conductance

The daily patterns of leaf conductance to water vapor at various times of the year are presented in Fig. 3. At no time was any appreciable nocturnal stomatal opening observed. Maximal stomatal opening (leaf water vapor conductance above 4 mm s^{-1}) was observed from January to May, after which soil water potential was very low (see Fig. 1). By May, partial stomatal closure occurred by midday and continued through the afternoon, when the water vapor pressure deficit was greatest. However, maximal leaf conductance (at 0800) was comparable in May to that ob-

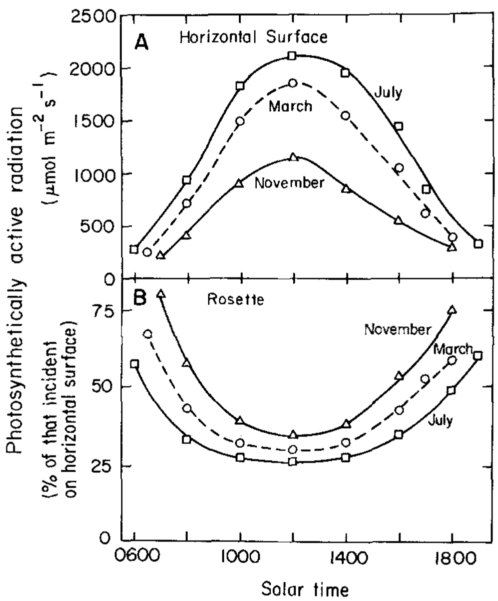

Fig. 2A, B. PAR incident on a horizontal surface (**A**) and the mean intercepted by individual leaf surfaces of a rosette (**B**) at three times during the study period: 17 November 1981, 23 March 1982, and 13 July 1982. Interception data are averaged for both sides of individual leaves and over the whole canopy, and are expressed as a percent of the PAR incident on a horizontal surface for the various dates

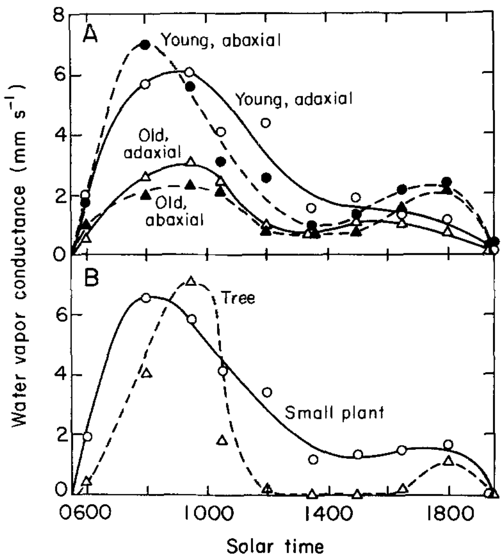

Fig. 4A, B. Water vapor conductance for various leaf surfaces on 18 May 1982: **A** water vapor conductance of the small plant (see Fig. 3) for different leaf ages (young, from upper part of rosette; and old, from lower part of rosette) and adaxial versus abaxial surfaces; and **B** mean water vapor conductance for the young, single-rosette plant compared to a rosette from a tree with 45 rosettes

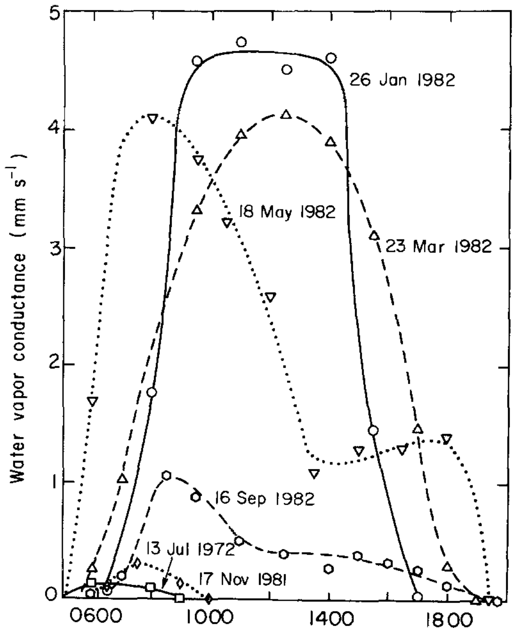

Fig. 3. Diurnal changes in water vapor conductance of *Yucca brevifolia* at various times

served in January and March (Fig. 3). By July, when water stress was apparently at its seasonal peak (see Fig. 1), stomatal closure was essentially complete, with only a slight early morning opening. Somewhat higher soil and leaf water potentials in September (Fig. 1) resulted in moderate stomatal opening, although after midday leaf conductance remained below 0.4 mm s^{-1}. As in July, the very dry period in November resulted in only brief stomatal opening in the morning (Fig. 3).

Leaf conductance varied with leaf age, plant age, and surface orientation. In May, leaf conductance was more than two-fold higher for young leaves than old leaves during the peak activity period in the morning (Fig. 4A). This was largely due to higher PAR interception by the young leaves, although at the same PAR older leaves had somewhat lower conductances. Within an age class, the adaxial surfaces exhibited slightly higher conductances through most of the day, although abaxial surfaces had higher conductances in the early morning and late afternoon, suggesting that incident PAR levels were the causative factor of these differences. Very similar results were obtained during the January observation period (data not shown). A comparison of the young plant rosette with the rosettes from a large tree during the May observation period (Fig. 4B) shows an approximately 4-h period of nearly complete stomatal closure for the tree compared to only partial closure at this time for the young plant. The absence of similar reductions earlier in the year may have been related to the production of flowers and fruits in May.

Photosynthesis and transpiration

The light responses of net photosynthesis for plants grown under low (20° C/9° C), moderate (31° C/17° C), and high (40°/25° C) day/night growth temperatures are shown in Fig. 5. *Yucca brevifolia* exhibited light saturation at a PAR of approximately 400 µmol m^{-2} s^{-1} for the low and high temperature regimes, but at about 600 µmol m^{-2} s^{-1} at the moderate temperature regime. Thus, *Y. brevifolia* exhibited light saturation at about 25% of maximum midday irradiance on a horizontal surface in the Mojave Desert.

The temperature responses of net photosynthesis, water vapor conductance, and CO_2 residual conductance in *Y. brevifolia* are presented in Fig. 6. The photosynthetic

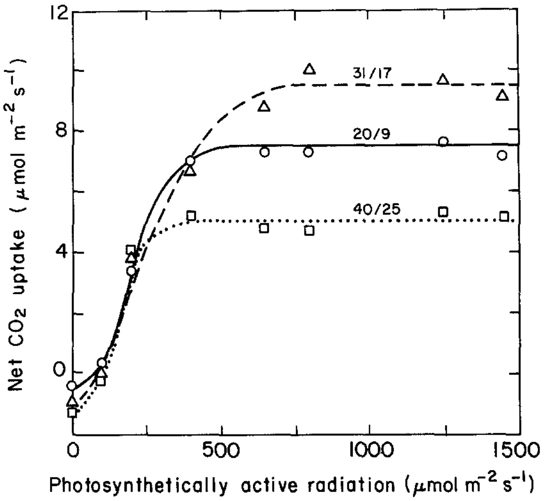

Fig. 5. Rate of net CO_2 exchange expressed on a total leaf area basis as a function of PAR for plants grown under 20° C/9° C, 31° C/17° C, and 40° C/25° C day/night air temperatures. Measurements were made at leaf temperatures equal to the daytime growth temperatures of the preconditioned plants

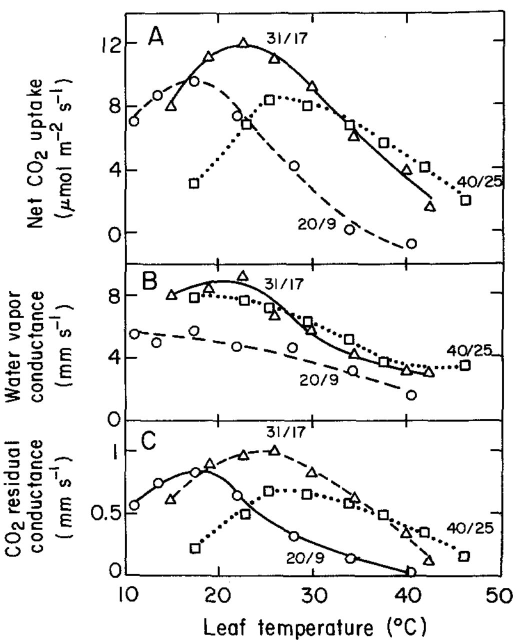

Fig. 6A–C. Effect of leaf temperature on net CO_2 exchange (**A**), water vapor conductance (**B**), and CO_2 residual conductance (**C**) at three growth temperatures (see Fig. 5). Measurements were made at light saturation (on both leaf surfaces) for each temperature regime

temperature optimum shifted from 17° C at the low temperature regime to 22° C at the moderate regime to 26° C at the high temperature regime. This represents a 4.5° C shift per 10° C change in daytime growth temperature and was accounted for primarily by a shift of the temperature dependence of the CO_2 residual conductance ($r = 0.98$ for all three growth temperatures analyzed together). Water vapor conductance was greatest at the lowest ambient temperatures tested at each growth temperature, except at the moderate temperature regime, where the optimum occurred at slightly over 20° C. Plants grown at the moderate temperature regime had the highest net photosynthesis of 12.0 μmol

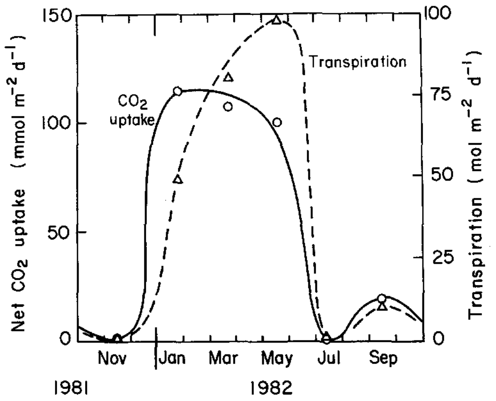

Fig. 7. Estimated daily net CO_2 uptake and transpiration for each field observation date

$m^{-2} s^{-1}$ versus a maximum of 9.6 μmol $m^{-2} s^{-1}$ for the low temperature regime and 8.5 μmol $m^{-2} s^{-1}$ for the high temperature regime. These plants also exhibited the highest net photosynthesis rate from 17° C to 32° C, and the highest CO_2 residual conductance from 17° C to 37° C. At 25° C, plants grown at the moderate temperature regime exhibited a net CO_2 uptake rate that was approximately 60% and 80% higher than that observed in the low and high temperature regime plants, respectively. Similarly, from 15° C to 40° C, the moderate temperature plants averaged 64% and 69% higher photosynthetic rates than did the low and high temperature plants, respectively.

Utilizing gas exchange data from the laboratory in concert with leaf conductances and microclimatic parameters from the field, the photosynthetic productivity and transpirational water loss of *Y. brevifolia* was estimated over a one-year period (Fig. 7). Leaf temperatures obtained in the field were used to predict residual CO_2 conductance (from Fig. 6). Water vapor conductances measured in the field for each leaf surface were then used to calculate the net CO_2 exchange, which was adjusted for the PAR incident on each leaf surface (using the photosynthetic responses in Fig. 5). Transpirational water loss was determined from water vapor conductances, measured leaf and air temperatures, and relative humidity for each measurement time. Net photosynthesis and transpiration rates, averaged over the whole canopy, were integrated from hourly data to obtain daily values (Fig. 7). Based on this analysis, which ignored nocturnal respiration, photosynthetic production was predicted to be greatest during the winter and spring wet season, with 80% of the seasonal CO_2 uptake occurring from January through May. Transpiration rose gradually from January to May, then dropped markedly during the subsequent periods of water stress. Stomatal control in September and November resulted in lower transpiration ratios (580 and 460 mol H_2O mol^{-1} CO_2, respectively) than in the more productive months of March and May (720 and 970, respectively). The extremely low leaf conductances observed in July make a prediction of transpiration ratio subject to large errors, so that the high estimated value of 1,630 may not be realistic. The lowest transpiration ratio of 390 was observed in January, when the highest seasonal water vapor conductances occurred in concert with moderate temperatures and low water vapor pressure deficits. When integrated over the whole year, the plant examined in this study had a predicted CO_2 uptake of

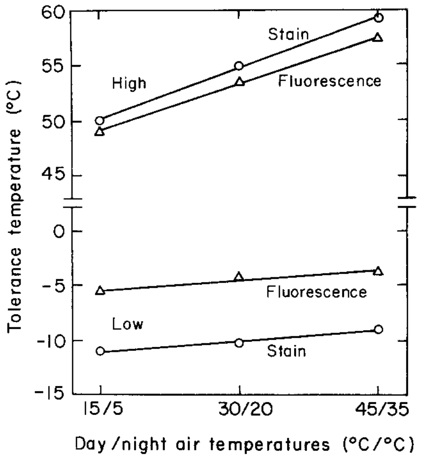

Fig. 8. High and low temperature tolerances of leaves measured for three different growth regimes. Tolerance temperatures were defined as the temperature for 50% inhibition of stain uptake or where the chlorophyll fluorescence increased substantially

21.6 mol m^{-2} y^{-1} and a transpirational water loss of 15,200 mol m^{-2} y^{-1}, resulting in a transpiration ratio of 700.

Temperature tolerances

The tissue temperature tolerances of *Y. brevifolia* and its ability to acclimate to changing growth temperatures were examined in the laboratory. High temperature tolerances were 57° C for the chlorophyll fluorescence rise and 59° C for stain uptake by mesophyll cells in plants grown at the highest day/night air temperatures employed, 45° C/35° C (Fig. 8). Acclimation to increasing growth temperatures from 15° C/5° C to 45° C/35° C averaged 2.8° C and 3.1° C per 10° C increase for chlorophyll fluorescence and stain uptake, respectively. Low temperature tolerances were −6° C for the chlorophyll fluorescence rise and −11° C for stain uptake in plants grown at the lowest day/night air temperatures, 15° C/5° C. Acclimation to decreasing growth temperatures from 45° C/35° C to 15° C/5° C averaged 0.6° C per 10° C decrease for chlorophyll fluorescence and 0.7° C per 10° C decrease for stain uptake (Fig. 8).

Discussion

Yucca brevifolia utilizes the C_3 pathway of photosynthesis, as has also been concluded from carbon isotope ratio analysis (Smith and Madhaven 1982). The species has both light and temperature responses typical of C_3 plants, and was here observed to have strictly daytime stomatal opening under all temperature regimes and water stress conditions. The maximum net CO_2 uptake rate was 12 μmol m^{-2} s^{-1} based on total leaf area (both sides; Fig. 6). This is about double that observed for other C_3 monocotyledonous rosette species from the Chihuahuan Desert (Kemp and Gardetto 1982) and other desert shrubs (Szarek and Woodhouse 1976, 1978), although similar to that observed for the most common North American desert evergreen, *Larrea divaricata* (*L. tridentata*; Mooney et al. 1978; the conventional rate is based on one leaf side only, and so it must be halved to compare with data based on total leaf area used here).

Photosynthesis in *Y. brevifolia* saturates at a relatively low PAR of 400 to 600 μmol m^{-2} s^{-1} (Fig. 5). In contrast, saturation does not occur until PAR levels approach full sunlight (about 2,000 μmol m^{-2} s^{-1}) for many other C_3 desert perennials, such as *Encelia farinosa* (Cunningham and Strain 1969) and *Larrea divaricata* (Reynolds et al. 1979). The low light saturation of photosynthesis in *Y. brevifolia* may be related to its rosette morphology, in which a relatively high leaf area index is maintained by a regular sequence of near-vertical leaf angles at the top of the rosette to near-horizontal at the bottom. At a high leaf area index, a canopy with vertical leaves in the upper layers and horizontal leaves below can optimize light utilization (Duncan 1971; Monsi et al. 1973). This pattern was observed here and resulted in a relatively even distribution of PAR throughout the canopy at most angles of solar elevation, as has also been observed in the rosettes of *Agave deserti* (Woodhouse et al. 1980). For the March PAR interception data (Fig. 2), an average of 35%, 21%, and 20% of the total daily PAR on a horizontal surface was intercepted by each leaf surface in the upper, middle, and lower parts of the *Y. brevifolia* rosette, respectively. Indeed, PAR interception added for both leaf surfaces is higher than that received on a horizontal surface at the beginning and end of the day (Fig. 2B). Other desert species, such as *Atriplex hymenelytra* (Mooney et al. 1977), also have steeply angled leaves and a low photosynthetic light saturation, suggesting that it may be a common adaptation in the high light environment of deserts. Other C_3 monocotyledonous rosette species may also have relatively low photosynthetic light saturation, as they tend to have a canopy architecture similar to *Y. brevifolia* and large leaf area indexes.

Yucca brevifolia exhibited one main peak in leaf diurnal water vapor conductance for all observation periods (Fig. 3). This is most common in C_3 plants with high photosynthetic rates and a well-watered condition, but is also observed in water-stressed plants with low CO_2 uptake rates (Schulze and Hall 1982). In the wet months of January and March, when leaf osmotic potential was at a maximum of about −1.0 MPa (Fig. 1), leaf conductance was at its highest level, exceeding 4 mm s^{-1} near midday. In May and September, when leaf osmotic potential fell to about −2.0 MPa, leaf conductance was maximal in the morning (~0800) and then dropped to a relatively constant value for the rest of the day. During extreme soil drought conditions in July and November, when leaf osmotic potentials averaged −3.0 MPa, only a brief morning peak of very low leaf conductance was observed. Thus, the leaf water vapor conductance pattern progressed from a broad peak of relatively high conductance centered at midday during periods of high water potential to a brief peak of very low conductance in the early morning at the times of maximum water stress. This differs from the two-peaked pattern of the C_3 shrub *Larrea divaricata*, which tends to exhibit a midday depression in leaf conductance throughout the year (Oechel et al. 1972).

The post-morning closure of stomata during times of high atmospheric water demand or low soil water potential is more complete in tree rosettes during flowering than in rosettes of young, unbranched plants (Fig. 4). This may be a function of greater leaf area and thus greater water loss in trees, or of water loss by reproductive structures which were abundant on trees during May. Leaf conductance was slightly higher on the adaxial surfaces than abaxial surfaces at midday but lower at the beginning and end of the day in both January and May (Fig. 4), reflecting the diurnal pattern of PAR interception.

The temperature optimum of photosynthesis shifted 4.5° C per 10° C change in growth temperature (Fig. 6), which would result in an overall 10° C to 12° C change in the temperature optimum over the range of temperatures experienced in the field. This is comparable to seasonal temperature acclimation in other desert perennials (Lange et al. 1974; Mooney et al. 1978; Badger et al. 1982) and in other C_3 yuccas from desert habitats (Kemp and Gardetto 1982). The maximum photosynthetic rate of *Y. brevifolia* changed as the temperature optimum did, being highest under moderate (31° C/17° C) growth temperatures. This differs from *Larrea divaricata*, which maintains a relatively constant maximum photosynthesis rate with acclimatory shifts in the temperature optimum (Mooney et al. 1978). The temperature acclimation response in *Y. brevifolia* was largely due to changes in the CO_2 residual conductance, rather than stomatal factors, and so can be ascribed to biochemical and/or biophysical factors at the mesophyll level, which is consistent with findings on many other species (e.g., Lange et al. 1974; Mooney et al. 1978).

The observed temperature acclimation of *Y. brevifolia* results in photosynthetic rates being within 20% of the maximum from 12° C to 22° C for the plants grown at low temperature (20° C/9° C), from 17° C to 29° C for the moderate temperature (31° C/17° C) plants, and from 23° C to 32° C for the high temperature (40° C/25° C) plants. Based on the prevailing temperatures prior to each field observation date and leaf temperatures during the observations, leaves would be at near optimum temperature (within 20% of maximum potential photosynthesis) for approximately 6 h per day in January, 10 h in March, 13 h in May, and 10 h in September; each optimum period overlapped the midday period. However, in July leaf temperatures near the optimum occurred for only 2 h (0700 to 0900) in the morning. Thus, photosynthesis by *Y. brevifolia* is better adapted to the moderate temperatures of spring and fall than to the high temperatures of summer. Furthermore, the temperature optimum of photosynthesis in desert plants can decrease up to 7° C to 10° C due to water stress (Nobel et al. 1978), so that temperatures in July would possibly be above the optimum range throughout the daylight period.

Yucca brevifolia can survive leaf temperatures well below 0° C and above 50° C, with a lower tolerance based on stain uptake of approximately −11° C and an upper tolerance of 59° C (Fig. 8). The respective tolerances of the photosynthetic apparatus, as measured by increases in the chlorophyll fluorescence rise, were −6° C and 57° C. This upper temperature is slightly higher than those observed for several other perennials of the Mojave Desert (Downton et al. 1980). *Yucca brevifolia* showed slightly greater sensitivity to both low and high temperature extremes compared with several species of *Agave* from the southwestern United States (Nobel and Smith 1983). Agaves tend to have much more massive leaves than does *Y. brevifolia*, resulting in leaf temperatures having a potentially greater departure from air temperature. Indeed, leaf temperatures of *Y. brevifolia* were within 2° C to 3° C of air temperature during both dry and wet conditions. Furthermore, the tendency for canopies of *Y. brevifolia* to occur well above the ground surface removes the leaves from its high temperature extremes, to which agaves are often fully exposed. As a result, leaf temperatures of *Y. brevifolia* appear not to reach their high temperature limit of 57° C or more in most Mojave Desert habitats. However, *Y. brevifolia* can occur in coniferous forest habitats above 2,000 m, where the lower temperature tolerance of −11° C may be a significant factor in determining its upward elevational limit.

Daily CO_2 uptake slightly exceeded 0.1 mol m^{-2} d^{-1} from January through May (Fig. 7), during which time 80% of the yearly CO_2 uptake occurred. In other months of the year, net CO_2 uptake was below 0.02 mol m^{-2} d^{-1}, and it was non-existent in July during the summer rainless period. Overall predicted yearly CO_2 uptake in *Y. brevifolia* was 22 mol m^{-2} y^{-1}. The plant's total leaf surface area of 1.66 m^2 leads to a CO_2 fixation of about 36 mol (1.58 kg) of CO_2. Assuming that 1 kg of CO_2 fixed leads to 0.68 kg dry weight, this would result in a productivity of approximately 1.07 kg dry weight, which is greater than the dry weight of the leaf canopy of 0.95 kg (Table 1). Since field observations indicate that only about 25% to 30% of the leaf rosette is replenished with new leaves in a given year, a large amount of carbohydrate is available for stem and root growth, maintenance respiration, and storage.

The annual water cost of carbon gain (the transpiration ratio) was 700 in *Y. brevifolia*. This is slightly high for C_3 plants (Osmond et al. 1982), and is higher than the transpiration ratio of 200 to 250 observed in several C_3 Sonoran Desert shrubs (Szarek and Woodhouse 1977). The seasonal increase in the transpiration ratio of *Y. brevifolia* with water stress is similar to that observed in the C_3 *Ceratoides lanata* in the Great Basin Desert, which varied from approximately 250 in the spring to well over 1000 in mid-summer (Caldwell et al. 1977). However, almost complete stomatal closure in *Y. brevifolia* throughout the dry summer period results in the mid-summer period having only a minor influence on yearly water loss and thus water cost of carbon gain.

In conclusion, the combination of a moderate photosynthetic rate and a high leaf area index enables *Y. brevifolia* to exhibit substantial productivity during the winter-spring growth period. Because photosynthetic light saturation occurs at a relatively low PAR level in this species and since rosette geometry results in a fairly uniform distribution of PAR, a large leaf surface area can be near light saturation during a majority of the day. Acclimation of the photosynthetic apparatus allows the optimal temperature for photosynthesis to be close to prevailing air temperatures for most of the year. Although the low temperature tolerance of its leaves may limit its range at higher elevations, the leaves of *Y. brevifolia* are apparently able to tolerate even higher temperatures than it encounters in the field. Stomatal control of water loss allows the leaves to be maintained during the summer and fall dry seasons. In this regard, while many other Mojave Desert perennials are drought-deciduous, *Y. brevifolia* retains an evergreen canopy.

Acknowledgements. We are grateful for the co-operation of Mr. Robert Moon of Joshua Tree National Monument and to Dr. Evan Romney for many useful discussions. Financial support was provided by U.S. Department of Energy contract DE-AM03-76-SF00012.

References

Badger MR, Björkman O, Armond PA (1982) An analysis of photosynthetic response and adaptation to temperature in higher

plants: temperature acclimation in the desert evergreen *Nerium oleander* L. Plant Cell Environ 5:85–99
Bender MM, Rouhani I, Vines HM, Blach CC (1973) $^{13}C/^{12}C$ ratio changes in Crassulacean acid metabolism plants. Plant Physiol 52:427–430
Benson L, Darrow RA (1981) Trees and shrubs of the southwestern deserts, 3d ed. University of Arizona Press, Tucson
Caldwell MM, White RS, Moore RT, Camp LB (1977) Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C_3 and C_4 species. Oecologia (Berlin) 29:275–300
Cunningham GL, Strain BR (1969) Irradiance and productivity in a desert shrub. Photosynthetica 3:69–71
Downton WJS, Seemann JR, Berry JA (1980) Thermal stability of photosynthesis in desert plants. Carnegie Inst Wash YB 79:143–145
Duncan WG (1971) Leaf angles, leaf area, and canopy photosynthesis. Crop Sci 11:482–485
Gentry HS (1980) The nature of *Yucca* and problems with their exploitation. In: Yucca, Centro de Investigación en Química Aplicada, Saltillo, Coahuila, Mexico, pp 125–133
Johnson HB (1975) Gas-exchange strategies in desert plants. In: Gates DM, Schmerl RB (eds) Perspectives in biophysical ecology, ecological studies Vol 12, Springer, New York, pp 105–120
Kemp PR, Gardetto PE (1982) Photosynthetic pathway types of evergreen rosette plants (Liliaceae) of the Chihuahuan Desert. Oecologia (Berlin) 55:149–156
Lange OL, Schulze E-D, Evenari M, Kappen L, Buschbom U (1974) The temperature-related photosynthetic capacity of plants under desert conditions. I. Seasonal changes of the photosynthetic response to temperature. Oecologia (Berlin) 17:97–110
Monsi M, Uchijima Z, Oikawa T (1973) Structure of foliage canopies and photosynthesis. Ann Rev Ecol System 4:301–327
Mooney HA, Ehleringer J, Björkman O (1977) The energy balance of leaves of the evergreen desert shrub *Atriplex hymenelytra*. Oecologia (Berlin) 29:301–310
Mooney HA, Björkman O, Collatz GJ (1978) Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata*. I. Carbon dioxide exchange characteristics of intact leaves. Plant Physiol 61:406–410
Munz PA (1974) A flora of southern California. University of California Press, Berkeley
Nobel PS, Hartsock TL (1978) Resistance analysis of nocturnal carbon dioxide uptake by a Crassulacean acid metabolism succulent, *Agave deserti*. Plant Physiol 61:510–514
Nobel PS, Hartsock TL (1979) Environmental influences on open stomates of a Crassulacean acid metabolism plant, *Agave deserti*. Plant Physiol 63:63–66
Nobel PS, Longstreth DJ, Hartsock TL (1978) Effect of water stress on the temperature optima of net CO_2 exchange for two desert species. Physiol Plant 44:97–101
Nobel PS, Smith SD (1983) High and low temperature tolerances and their relationships to distribution for agaves. Plant Cell Environ (in press)
Oechel WC, Strain BR, Odening WR (1972) Photosynthetic rates of a desert shrub, *Larrea divaricata* Cav., under field conditions. Photosynthetica 6:183–188
Onwueme IC (1979) Rapid, plant-conserving estimation of heat tolerance in plants. J Agr Sci Camb 92:527–536
Osmond CB, Winter K, Ziegler H (1982) Functional significance of different pathways of CO_2 fixation in photosynthesis. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology, new series, Vol 12B, Springer, Berlin, pp 615–675
Reynolds JF, Cunningham GL, Syvertsen JP (1979) A net CO_2 exchange model for *Larrea tridentata*. Photosynthetica 13:279–286
Schreiber U, Berry JA (1977) Heat-induced changes of chlorophyll fluorescence in intact leaves correlated with damage of the photosynthetic apparatus. Planta 136:233–238
Schulze E-D, Hall AE (1982) Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology, new series, Vol 13B, pp 181–230
Smith BN, Madhaven S (1982) Carbon isotope ratios in obligate and facultative CAM plants. In: Ting IP, Gibbs M (eds) Crassulacean acid metabolism, Waverly Press, Baltimore, pp 231–243
Syvertsen JP, Nickell GL, Spellenberg RW, Cunningham GL (1976) Carbon reduction pathways and standing crop in three Chihuahuan Desert plant communities. Southwest Nat 21:311–320
Szarek SR, Troughton JH (1976) Carbon isotope ratios in Crassulacean acid metabolism plants. Seasonal patterns from plants in natural stands. Plant Physiol 58:367–370
Szarek SR, Woodhouse RM (1976) Ecophysiological studies of Sonoran Desert plants. II. Seasonal photosynthesis patterns and primary production of *Ambrosia deltoides* and *Olneya tesota*. Oecologia (Berlin) 28:365–375
Szarek SR, Woodhouse RM (1978) Ecophysiological studies of Sonoran Desert plants. IV. Seasonal photosynthetic capacities of *Acacia greggii* and *Cercidium microphyllum*. Oecologia (Berlin) 37:221–229
Woodhouse RM, Williams JG, Nobel PS (1980) Leaf orientation, radiation interception, and nocturnal acidity increases by the CAM plant *Agave deserti* (Agavaceae). Am J Bot 67:1179–1185

Received April 18, 1983